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CHEMOTAXIS OF OYSTER DRILLS *UROSALPINX CINEREA* TO COMPETING PREY ODORS

LESLIE G. WILLIAMS,[1] DAN RITTSCHOF,[2] BETSY BROWN[3] AND MELBOURNE R. CARRIKER

University of Delaware, College of Marine Studies, Lewes, DE 19958

ABSTRACT

Response of newly hatched, predatory snails to competing chemical cues from co-occurring species of prey were determined in laboratory experiments. Egg capsules of *Urosalpinx cinerea* were collected from an intertidal, vertically zoned community of prey species. The most prevalent prey were barnacles *Semibalanus balanoides* and *Balanus eburneus,* oysters *Crassostrea virginica,* mussels *Mytilus edulis,* and bryozoans *Membranipora tenuis* and *Schizoporella irrorata.* Snail chemotaxis evoked by barnacle odor alone and barnacle odor mixed with odor of either mussels or oysters was assayed in an activity chamber. Mussel odor inhibits chemotaxis to barnacles, but does not evoke chemotaxis itself. Oyster odor inhibits chemotaxis to high concentrations of barnacle odor, but increases chemotaxis to low concentrations of barnacle odor. Chemotaxis to barnacle odor is reduced by 2 h pre-exposure to either barnacle, oyster, or mussel odors. Such cross-adaptation suggests that inhibition or facilitation of chemotaxis in odor mixtures is not caused by one odor masking a second while free in the sea water. We infer that newly hatched snails integrate chemical information in barnacle-oyster and barnacle-mussel odor mixtures. These results, and those of earlier investigations, suggest a behavioral explanation for vertical distribution of juvenile *U. cinerea* in the intertidal zone.

INTRODUCTION

Predators that actively search for food usually show some degree of specificity in what they will and will not eat. Specificity depends on a fundamental aspect of animal behavior, the ability to integrate a spectrum of sensory information and respond only to those cues that are meaningful. Previous studies in our laboratory have shown that balanoid barnacles produce a potent chemical cue that evokes search behavior in both newly hatched and adult *Urosalpinx cinerea* (Say) (Rittschof *et al.,* 1983). *Crassostrea virginica* (Gmelin), however, produce a stimulus that is weakly attractive to newly hatched *U. cinerea* (Rittschof *et al.,* 1983) but is strongly attractive to those snails that have fed upon *C. virginica* (Wood, 1968; Wood *et al.,* 1983). *Mytilus edulis L.* do not seem to evoke chemotactic search behavior at all, though they constitute a major source of prey for *U. cinerea* in some areas (Wood, 1968). This study examines behavioral integration of competing chemical cues by measuring chemotactic orientation of the predatory snail *U. cinerea* to mixtures of prey odor.

Urosalpinx cinerea is a shell-boring, muricid gastropod endemic to the Atlantic Coast of North America (Carriker, 1955). Throughout its range *U. cinerea* occupies rocky and shellbed habitats below the mid-tidal line where it preys upon numerous

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[1] Present Address: Department of Botany KB15, University of Washington, Seattle, WA 98195, [2]Duke University Marine Labs, Pivers Island, Beaufort, NC 28516, and [3]Battelle Marine Research Laboratory, 397 Washington St., Duxbury, MA 02332.

species of sessile, shelled, and encrusting invertebrates, many of which are commercially valuable. The list of prey includes at least 20 species of bivalves, gastropods, barnacles, bryozoans, and small decapod crustaceans (Carriker 1955; Hancock, 1959; Franz, 1971; Pratt, 1974; and Ordzie and Garofalo, 1980). In contrast to the diversity of prey species attacked throughout its range, *U. cinerea* tends to be a stenotrophic predator within its microhabitat, detecting and selecting preferred species of prey by odor (Cole, 1944; Haskin, 1950; Hancock, 1959; Wood, 1968; Pratt, 1974; Ordzie and Garofalo, 1980; Rittschof *et al.,* 1983). In general, prey preference by *U. cinerea* is hierarchical, headed by balanoid barnacles and followed in order by oyster spat and mussels. Finally, *U. cinerea* has also evolved the capability of switching to other species of prey when its preferred prey becomes rare or is no longer available (Wood, 1968). Wood (1968) concludes that prey switching is a result of: 1) population density and distribution of prey, and 2) recent ingestive experience of the predator (*i.e.,* ingestive conditioning).

The role of chemoreception in orientation to prey, prey preference, and prey switching behaviors is complex. Chemotaxis of *Urosalpinx cinerea* toward several, but not all, prey species is an innate behavior. Newly hatched, and ingestively naive, *U. cinerea* are attracted to odors emanating from young hardshell clams [*Mercenaria mercenaria* (L.)], barnacles [*Semibalanus balanoides* (L.) and *Balanus eburneus* Gould], bryozoans [*Schizoporella irrorata* (Watess) and *Membranipora tenuis* Desor], an oyster [*Crassostrea virginica* (Gmelin)], and the tube dwelling polychaete *Sabellaria vulgaris* Verill (Carriker, 1957; Rittschof *et al.,* 1983). Adult *U. cinerea* can chemolocate prey species such as the bay scallop *Argopecten irradians* (Lamarck) that do not evoke chemotaxis in newly hatched snails (Ordzie and Garofalo, 1980; Rittschof *et al.,* 1983). Several species of prey such as slipper limpets *Crepidula fornicata* (L.) and mussels *Mytilus edulis* are not chemotactically located from a distance by either newly hatched or adult *U. cinerea* (*c.f.,* Pratt, 1974 and Rittschof *et al.,* 1983), though both species are attacked and eaten by the snails. In the case of *C. fornicata,* Pratt (1974) further demonstrated that attack (*i.e.,* shell penetration and feeding) was evoked by a chemical cue.

The purpose of this investigation was to determine how *Urosalpinx cinerea* behaviorally integrates competing chemical cues from several co-occurring species of prey, barnacles (*Semibalanus balanoides* and *Balanus eburneus*), oysters (*Crassostrea virginica*), and mussels (*Mytilus edulis*). Better understanding of integration of competing chemical cues is important for further insight into: 1) prey preference and switching behaviors; 2) prey location in an often turbulent aquatic environment where odors of several spatially separate prey species may be mixed; and 3) unique aspects of orientation to prey, though the overall behavioral response, predation, is the same. We addressed the problem by measuring the effects that oyster and mussel odors have on chemotaxis of *U. cinerea* to barnacle stimulus. This was done by comparing snail chemotaxis evoked by individual species odors with that evoked by odor mixtures. Effects of odor mixtures on snail chemotaxis were further quantified by measuring: 1) adaptation of *U. cinerea* to single odor on later response to that odor; and 2) adaptation to one odor on response to a second odor (*i.e.,* cross-adaptation).

Materials and Methods

Collection and culture of Urosalpinx cinerea

Egg capsules of *Urosalpinx cinerea* were collected near mean low water (MLW) from the inner breakwater of Delaware Bay at Lewes, Delaware (38° 47′ N, 75° 06′

W). Capsules were transported to the laboratory in sea water, cleaned of debris by washing on a 3 mm mesh screen, and incubated in filtered sea water as described by Rittschof *et al.* (1983). Newly hatched *U. cinerea* were removed from culture dishes several times a week, and were usually used for experiments within a day of collection. Experimental snails were used only once and therefore were naive in the sense that they neither fed upon nor were exposed to prey prior to an experiment.

Field observations

In August and September, 1980, careful observations were made of the intertidal zone from the site of egg-capsule deposition (about 0.5 m below MLW) to the approximate upper limit of distribution of the barnacle *Semibalanus balanoides* (about 3 m above MLW). Relative position of various potential prey of *Urosalpinx cinerea* was noted, and the prey and substrata searched for recently hatched snails.

Prey species and odor preparation

The four prey species used were *Mytilus edulis, Crassostrea virginica, Semibalanus balanoides,* and *Balanus eburneus.* The barnacles and mussels were collected from the inner breakwater at the time of collection of *Urosalpinx cinerea* egg-capsules. Oysters were removed from a raft culture maintained in the Broadkill estuary, Lewes, Delaware. Specimens were brought into the laboratory, placed in small aquaria (5–40 liters), aerated, and supplied with filtered (0.5 μm) sea water (about 32‰). These animals were used within a week of capture to prepare odor-bearing water for our various experiments. Animals not used within a week of capture were caged in the Broadkill estuary where they could be retrieved for later experimentation.

Odor was prepared by placing unfouled specimens of each prey species into separate 5 liter aquaria containing filtered sea water. Aquaria were bubbled with air overnight. Water was siphoned from each aquarium, filtered through a glass fiber filter (Whatman GF/F), and in some instances refiltered through polycarbonate membrane filters (0.4 or 0.2 μm, BioRad, Inc.). In some instances the stimulus water was frozen in 100 ml polycarbonate containers and thawed prior to use. Stimulus preparation and determination of stimulus potency is reported in more detail by Rittschof *et al.* (1983).

Bioassay procedure

Assay Device. Distance chemotaxis was measured in an assay device consisting of a reservoir of stimulus solution held in a 500 ml mariotte flask, a 2 ml calibrated pipette bent into an elbow at one end, and an intervening flow meter (Gilmont, Inc.). Four to six devices were run simultaneously. During each experiment, 15 to 30 newly hatched snails were transferred from 20 ml vials into the open mouth of each pipette with a small paint brush, and allowed 30 s to attach to the interior surface of the pipette. Stimulus flow was then started and adjusted to the optimum discharge rate of 7.5 ml/min (approximately 75 cm/min linear velocity). Further details of methods are reported by Rittschof *et al.* (1983).

Chemotaxis. The assay required an all-or-none type of response from the snails. The response criterion chosen was upstream movement of at least 1 cm within 10 min after restarting the stimulus flow (Rittschof *et al.,* 1983). Since homogeneous stimulus solutions were used in this study, there was no chemical gradient to direct the snails' responses. Responses to the various chemical cues were determined by

comparison of their active upstream migration in odor-laden currents of water with their relative inactivity under identical, odor-free conditions of flow. Therefore, the behavior assayed was a non-random, chemically stimulated rheotaxis, which will be referred to as chemotaxis in this paper.

Mixed stimulus experiments

Mussel-Barnacle. In two experiments, we compared chemotaxis of *Urosalpinx cinerea* to barnacle odor (*Balanus eburneus*) with that evoked by a mixture of barnacle and mussel odors. The same stimuli were used in each experiment. Barnacle odor was prepared ahead of time by filtration (0.4 μm), and rapid freezing of 100 ml aliquots on dry ice. Mussel odor was prepared fresh by filtering it through Whatman GF/F and 0.4 μm polycarbonate filters, and cooling the filtrate on ice until needed. We then measured chemotaxis of *U. cinerea* to a range of dilutions of barnacle stimulus in order to establish expected frequencies of response for the subsequent mixed odor experiments. Chemotaxis evoked by 1.0% and 5.0% (v/v) dilutions of barnacle stimulus in each of a set of four dilutions of mussel stimulus (10.0, 5.0, 1.0, and 0.5% v/v and 10.0, 4.0, 1.0, and 0.1% v/v respectively) was measured. Stimulus strength was calculated as the percentage of volume of stimulus water in the total volume of solutions.

Oyster-Barnacle. Two series of experiments were conducted to assess the effect of oyster odor on the chemotactic response of *Urosalpinx cinerea* to barnacle odor. In the first series, three experiments were performed to establish the snails' response to various dilutions of: 1) barnacle odor alone (*Semibalanus balanoides;* 10.0, 2.0, 1.0, and 0.5%); 2) oyster odor alone (100, 10.0, 1.0, and 0%) and 3) barnacle odor mixed with 100% oyster odor (10.0, 1.0, 0.5, and 0%). The barnacle odor was the same for each experiment, and was prepared in advance by filtration (0.4 μm) and freezing on dry-ice. Oyster odor was made by placing 5 oysters (total wet wt = 119.1 g) in 3 liters of sea water for 3 h, siphoning the sea water from the aquarium, and filtering it through glass fiber filters (Whatman GF/F).

In the second series, four experiments measured the effects of different concentrations of concurrent oyster odor on the response to barnacle odor (*Balanus eburneus*). The first experiment measured the response to 5.0, 2.0, 1.0, and 0.7% dilutions of barnacle odor mixed in 95% oyster odor. The second, third, and fourth experiments measured the response to the four dilutions of barnacle odor mixed in 10, 1.0, and 0.1% oyster odor respectively. The same batch of filtered and frozen barnacle stimulus was used in each experiment, and was prepared as described for the mussel-barnacle experiments. Oyster stimulus was prepared by allowing 8 oysters to pump in an aquarium containing 5 liters of filtered sea water for 3 h. The water was siphoned from the aquarium, filtered (GF/F), and cooled in an ice bath.

Adaptation experiments

This experiment examined the effects of prolonged exposure to *Semibalanus balanoides* odor on chemotaxis of newly hatched *Urosalpinx cinerea.* Barnacle odor, which had been filtered and frozen, was thawed, diluted, and warmed to 22°C immediately before use in this experiment. Snails were apportioned into 2 groups of about 300 snails each, and caged in 2 20 ml plastic vials. The vials were screened at both ends to permit circulation of sea water. One vial was submerged in a 10% dilution of barnacle stimulus and the second in filtered sea water (GF/F). After 2 h, a sample of snails from each treatment was assayed in a dilution series of barnacle stimulus (10.0, 1.0, 0.5, and 0%).

Cross-adaptation experiments

Two experiments were performed to test the effects of 2 h pre-exposure to oyster and mussel odors on chemotaxis to barnacle (*Balanus eburneus*) odor. In the first experiment, snails were divided into groups of 300 snails, and each group caged in a screened, 20 ml vial. Vials were then submerged for 2 h in either undiluted oyster stimulus, mussel stimulus, barnacle stimulus or filtered sea water. Samples of snails from each vial were then assayed for their response to 1% and 10% barnacle odor.

Lastly, the effect of 2 h pre-exposure to filtered sea water, oyster, mussel, and barnacle odors on the response to 10% dilutions of either oyster or mussel odors was determined. The various odors for these experiments were filtered (GF/F), frozen, and stored at −20°C. Prior to each experiment, the frozen samples were thawed, filtered (0.4 μm), and diluted, when appropriate, with similarly filtered sea water.

Statistics

The effect of stimulus dilution on chemotaxis was tested for significance by means of the log-likelihood ratio or G-test (Sokal and Rohlf, 1969). Data were further analyzed by calculating the proportion (P) of snails responding to each dilution, and then by regression of the angle of P (angle = arcsin of the square root of P) on the log of stimulus dilution. The angular transformation is helpful in simplifying a curvilinear relationship into a linear one, particularly where very high (>70%) or very low (<30%) frequencies of response occur.

Results

Field Observations

The inner breakwater of Delaware Bay is vertically zoned with respect to distribution of potential prey of *Urosalpinx cinerea. Semibalanus balanoides* occurs in the upper intertidal and intergrades with the top of the upper end of the *Mytilus edulis* zone at about 50 cm above mean low water (MLW). A small population of *Crassostrea virginica* occupies a narrow zone 40–60 cm above MLW. Bryozoans, chiefly *Membranipora tenuis* and *Schizoporella irrorata,* occur about 50 cm below MLW, at about the same elevation as egg capsules of *U. cinerea.* Newly hatched snails (less than 2 cm axial length) were observed below MLW at the bases of egg capsules, upon the shells of adult *U. cinerea,* and upon barnacle, mussel, and bryozoan prey. Adult snails were found as high as 100 cm above MLW.

Mixed stimulus experiments

Mussel-Barnacle. Mussel odor inhibits the response of *Urosalpinx cinerea* to odor of *Balanus eburneus.* In each of two experiments conducted, the response of newly hatched snails to barnacle odor alone was significantly associated with stimulus dilution ($P < 0.005$). Data pooled from these experiments show an increase in frequency of response to barnacle odor as a function of increasing stimulus strength (Fig. 1). This relationship predicts 33% and 15% responses to 5% and 1% dilutions of barnacle odor respectively. Response to 1% barnacle odor mixed with varying concentrations of mussel odor began to decrease significantly ($P < 0.005$) from the predicted 15% response with increasing concentration of mussel stimulus (Fig. 2). Response to 5% barnacle odor mixed with mussel odor also declined significantly ($P < 0.05$) below the 33% predicted response.

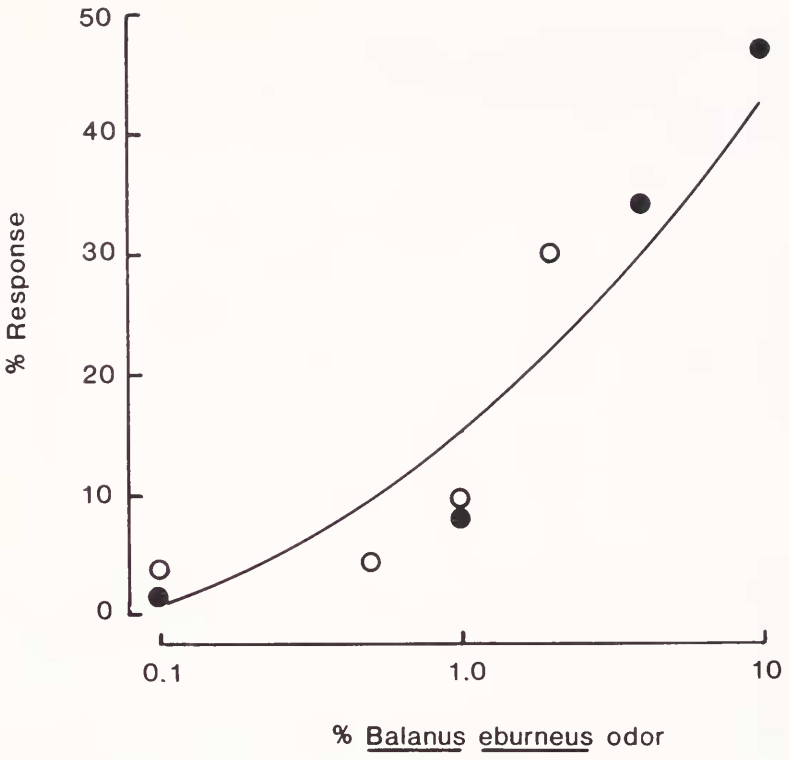

FIGURE 1. Frequency of reponse of newly hatched *Urosalpinx cinerea* to *Balanus eburneus* odor (BEO) plotted as a function of stimulus dilution. The curve was fitted from the regression equation

$$\text{Arcsin } P = 17.6 \log (\text{BEO}) + 58.1$$

with a coefficient of determination of 0.842. P = the proportion of snails responding. Open and closed symbols represent experiments performed several hours apart. Sample size for each data point ranged from n = 64 to n = 81 snails.

Oyster-Barnacle. Chemotaxis of newly hatched snails to either barnacle (*Semibalanus balanoides*) odor, oyster odor, or a mixture of the two was significantly associated with stimulus dilution in each case ($P < 0.05$). Frequency of response increased with increased strength of barnacle and oyster stimuli. However, both rate of increase and magnitude of response was greater for snails exposed to barnacle odor than for those exposed to oyster odor. Response to dilutions of barnacle odor mixed with 100% oyster odor was intermediate, both in magnitude and in rate of increase, to that evoked by barnacle or oyster odors individually (Fig. 3). In the second series of four experiments that measured response to a range of concentrations of barnacle (*Balanus eburneus*) odor mixed in various dilutions of oyster odor (95, 10, 1.0, and 0.1%), the overall chemotactic response was dominated, as expected, by barnacle odor ($G = 80.06$, $P < 0.005$). However, oyster odor had a significant effect on chemotaxis at 3 of the 4 concentrations of barnacle odor (Table 1). Oyster odor inhibited the response evoked by 5% barnacle odor, and either facilitated or remained neutral to the response evoked by lower dilutions of barnacle odor.

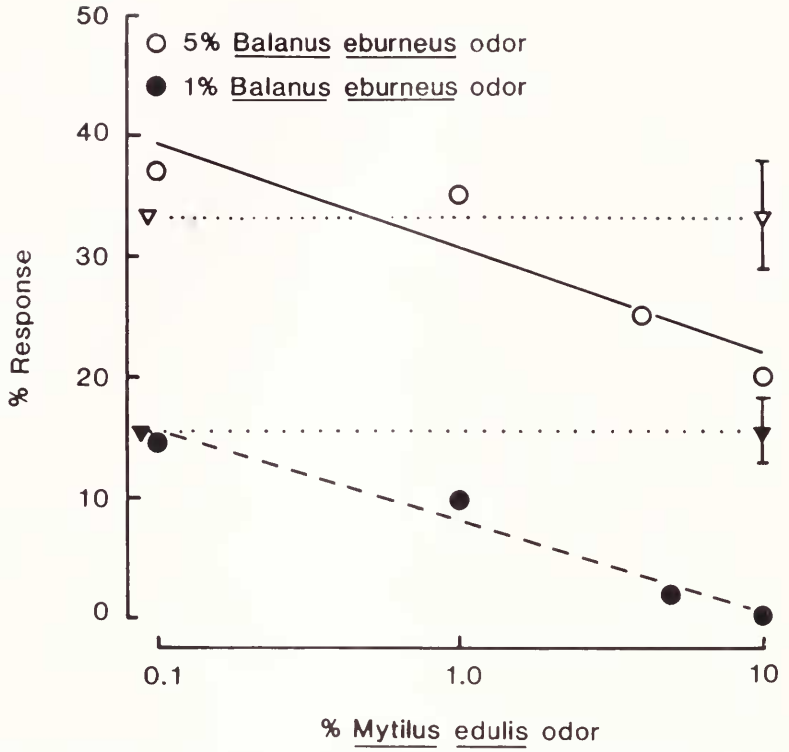

FIGURE 2. Response of *Urosalpinx cinerea* to a mixture of *Balanus eburneus* and *Mytilus edulis* odors, and plotted as a function of *M. edulis* stimulus dilution. Inverted triangles and dotted lines show the % response (±1 standard deviation) predicted from the control experiment shown in Figure 1. Negative slope of lines fitted to data indicate that *M. edulis* inhibits chemotaxis to *B. eburneus*. Sample size at each dilution of *M. edulis* odor ranged from n = 67 to n = 81.

Adaptation experiment

Chemotaxis of *Urosalpinx cinerea* was significantly associated with dilution of *Semibalanus balanoides* odor ($P < 0.005$) as well as with prior exposure to barnacle odor ($P < 0.005$). As hypothesized, pre-exposure to barnacle stimulus decreased the response of the snails, but only at the lower concentrations of barnacle odor (Fig. 4). Pre-exposure to 10% barnacle odor did not significantly affect response of the snails to either 10% barnacle odor or filtered sea water (*i.e.*, rheotaxis).

Cross-adaptation experiments

There was a highly significant ($P < 0.005$), concentration dependent association between chemotaxis of snails to barnacle odor and their prior exposure to filtered sea water, or oyster, mussel, and barnacle odors. As anticipated in the foregoing adaptation experiments, chemotaxis to barnacle odor was least for snails exposed to filtered sea water. This generalization is true for snails responding to either 10% or 1% barnacle odor, the only difference being in magnitude of response (Fig. 5).

TABLE I

Contingency table summarizing the effects of Crassostrea virginica *odor (CVO) on chemotaxis of* Urosalpinx cinerea *to each of 4 concentrations of* Balanus eburneus *odor (BEO)*

Exp.	BEO (%)	CVO (%)	Response	N	% Response	Overall-G	*P*
1	5.0	95	29	66	44		
1	5.0	10	37	61	61		
1	5.0	1.0	63	94	67		
1	5.0	0.1	44	66	67	10.14	<0.005
2	2.0	95	30	42	71		
2	2.0	10	27	63	43		
2	2.0	1.0	40	88	45		
2	2.0	0.1	28	63	44	10.63	<0.010
3	1.0	95	16	64	25		
3	1.0	10	10	55	18		
3	1.0	1.0	33	90	37		
3	1.0	0.1	22	61	36	7.68	>0.050
4	0.7	95	21	49	43		
4	0.7	10	25	71	35		
4	0.7	1.0	18	74	24		
4	0.7	0.1	9	62	15	13.53	<0.005

Stimulus strength is expressed as a percentage of the volume of stimulus water in the total volume of stimulus solution. Tests for significance of association between chemotaxis and strength of oyster odor are summarized as Overall-G for each concentration of barnacle odor.

Snails pre-exposed to oyster or mussel odors showed greater response to barnacle odor than those pre-exposed to barnacle odor, but showed a lower response than those pre-exposed to filtered sea water.

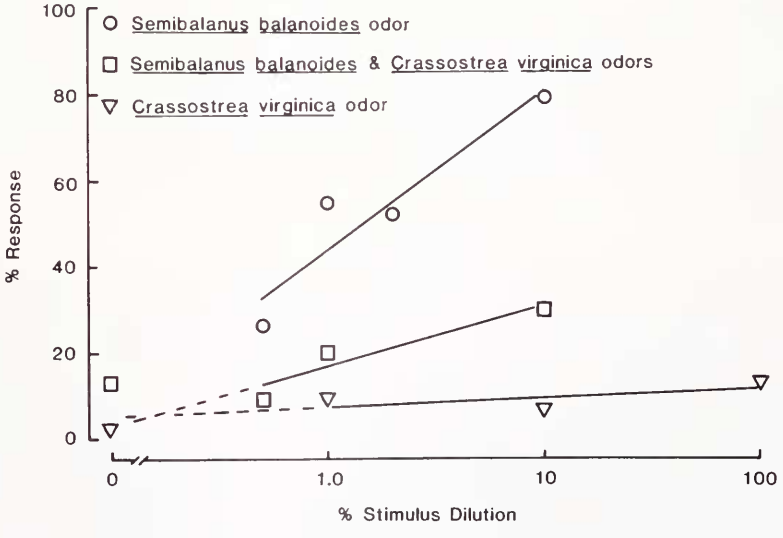

FIGURE 3. Response of Urosalpinx cinerea to dilutions of mussel or oyster odor, or to a mixture of the two. Lines fitted by least squares regression of % response on log of stimulus dilution. Zero (*i.e.*, control) values were omitted from the regression because such values are incompatible with the logarithmic transformation. Sample size for the various data points ranged from n = 61 to n = 71 (*Semibalanus balanoides*), n = 67 to n = 73 (*Crassostrea virginica*), and n = 55 to n = 68 (*S. balanoides* + *C. virginica*).

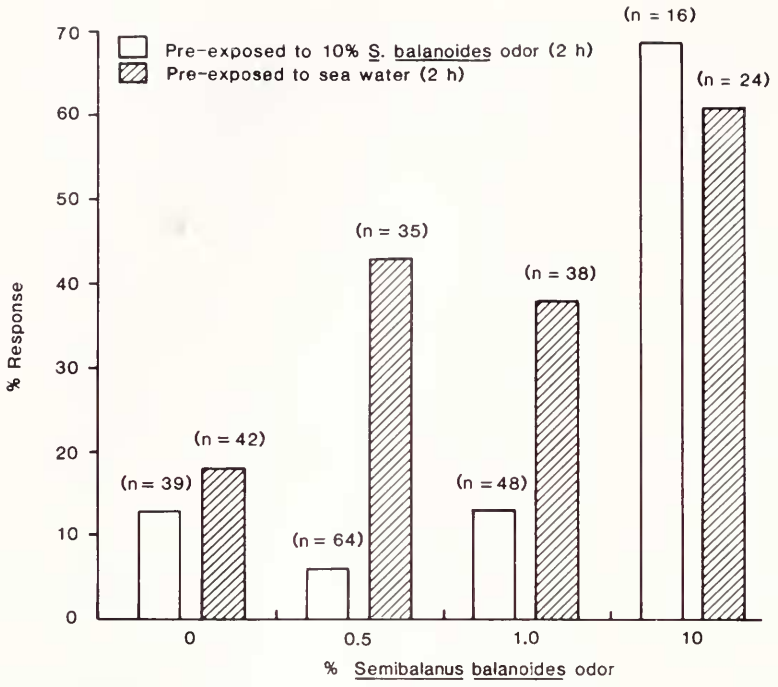

FIGURE 4. Effect of 2 h exposure to either 10% *Semibalanus balanoides* odor or sea water on chemotaxis of *Urosalpinx cinerea* to barnacle odor. Sample size for each treatment shown in parentheses.

Cross-adaptation effects are less clear in the case of response to mussel or barnacle odors following pre-exposure of snails to sea water, or barnacle, mussel, and oyster odors (Fig. 6). Chemotaxis to 10% oyster odor was equally and significantly ($P < 0.05$) depressed for snails pre-exposed to the 3 odors. Chemotaxis to 10% mussel odor was unaffected by pre-exposure to barnacle or mussel odors, but depressed by pre-exposure to oyster odor (Fig. 6).

DISCUSSION

Our mixed prey experiments reaffirm the chemotactic potency of barnacle odor for newly hatched *Urosalpinx cinerea,* and further show that chemical cues emanating from *Mytilus edulis* and *Crassostrea virginica* significantly affect the chemotactic response of *U. cinerea* to barnacle odor. Moreover, concentration-dependent differences in chemotaxis to the various mixtures suggest qualitative differences among the three stimuli. Mussel odor alone does not evoke chemotaxis, but inhibits response to all concentrations of barnacle odor. Oyster odor inhibits the response to high concentrations of barnacle odor but facilitates the response to low concentrations of barnacle odor. It must be emphasized that the response to oyster odor mixed with low concentrations of barnacle odor (0.7%) exceeded that anticipated to oyster odor alone (*i.e.,* about 20% maximally). This observation suggests that the interaction of oyster and barnacle odors at these concentrations may be additive or synergistic (Fig. 3, Table I).

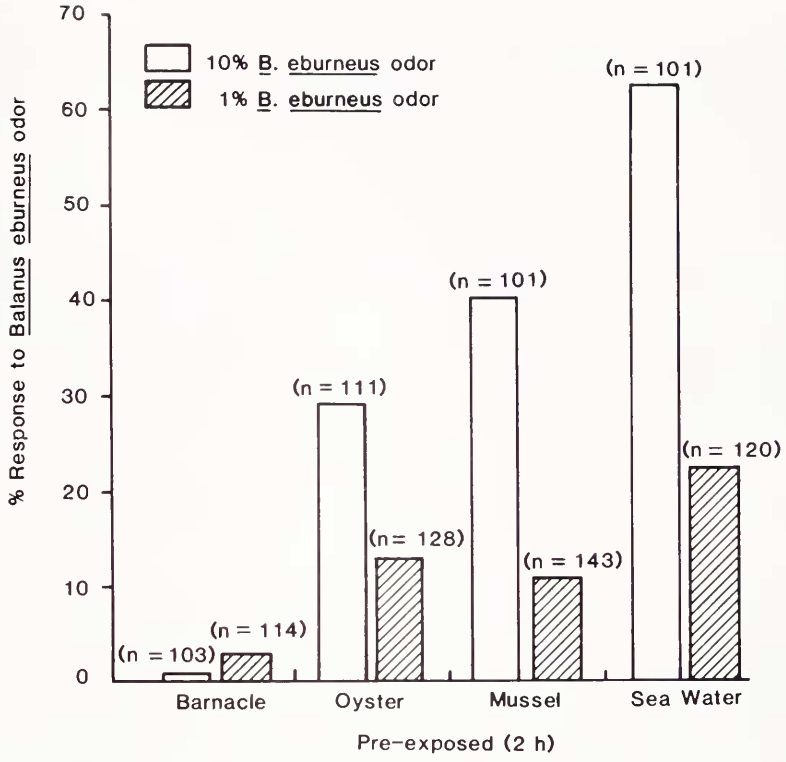

FIGURE 5. Cross-adaptation experiment. Chemotaxis of newly hatched snails to 1% and 10% barnacle odor following 2 h pre-exposure to *Balanus eburneus, Crassostrea virginica,* or *Mytilus edulis* odors or to sea water. Sample size shown above bars in parentheses.

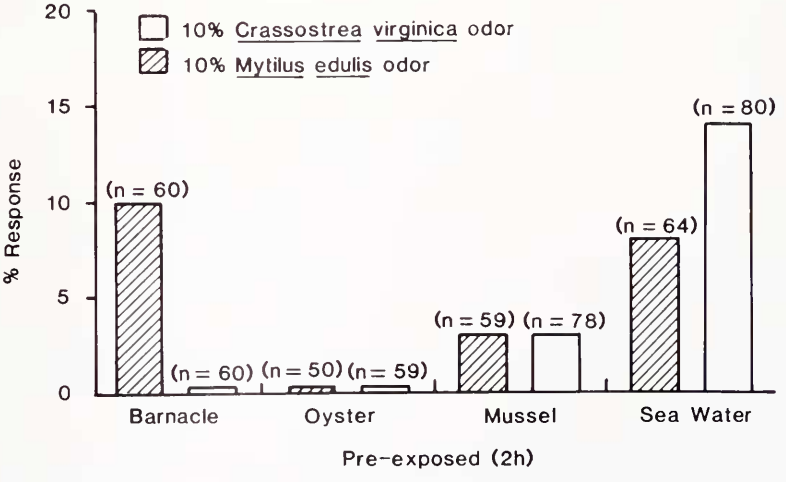

FIGURE 6. Chemotaxis of newly hatched *Urosalpinx cinerea* to 10% oyster and mussel odors following 2 h pre-exposure to either filtered sea water, or *Balanus eburneus, Crassostrea virginica,* or *Mytlius edulis* odors. Sample size shown above bars in parentheses.

If the three odors are chemically the same, we would expect reduced chemotaxis to oyster and mussel odors following pre-exposure of snails to barnacle odor. However, pre-exposure to barnacle odor inhibited chemotaxis to oyster odor but not to mussel odor (Fig. 6). Also, we would not expect inhibition (*i.e.,* cross-adaptation) of chemotaxis to a strong barnacle stimulus (*i.e.* one that evokes a 60% response, Fig. 5) following pre-exposure to weak oyster or mussel odors, neither of which evokes more than a 20% response. Clearly, these weak chemotactic odors are capable of inhibiting the response to the much more powerful barnacle odor, again suggesting that the three are indeed different. These results suggest that the effects of stimulus mixtures on chemotaxis are perceptual or behavioral, and not a result of one stimulus masking a second while free in the sea water. Perceptually, cross-adaptation could be explained by any one of several mechanisms; sensory adaptation, sensory fatigue, or stimulus filtering (Hinde, 1966). Similarly, at the behavioral level, cross-adaptation could be explained by response specific fatigue (Manning, 1979), or by generalized habituation to several stimuli (Petrinovich, 1973; Wyers *et al.,* 1973). However, habituation is an unsatisfactory explanation of snail chemotaxis in odor mixtures because the 10 min period of our bioassay is too brief to bring it about (LGW and BB, unpublished observations).

More importantly, results concerning response to odor mixtures offers new insight into mechanisms of orientation, location, and preference of prey. Wood (1968) and Wood *et al.* (1983) demonstrated that odor of *Crassostrea virginica* may become as attractive as odor of *Balanus* spp to *Urosalpinx cinerea,* but only if *U. cinerea* had previously fed upon *C. virginica* for a period of time. Wood (1968) speculated that this change in response to oyster odor could be a form of associative learning if a novel olfactory stimulus were paired with reinforcement offered by ingestion of oyster flesh. From this study as well as that of Wood (1968), Wood *et al.* (1983), and Rittschof *et al.* (1983), it seems that the criterion of simultaneous olfactory stimulation by a novel stimulus associated with food has been satisfied. This type of associative process could also account for the switching behavior of another predatory, shell-boring gastropod, *Acanthina spirata* (Blainville) (Murdoch, 1969). This type of olfactory plasticity appears quite common and has been identified in orientation to prey by terrestrial snails (Croll and Chase, 1980) and tuna (Atema *et al.,* 1980), and in orientation to host symbionts by pea crabs (Derby and Atema, 1980) and scale worms (Dimock and Davenport, 1971).

Lastly, we hypothesize that vertical migration of newly hatched snails is affected by prey odors primarily through interaction with one another and with abiotic factors (water current and gravity). Egg capsules in newly hatched snails occur subtidally, near MLW, 100 cm or more below the upper (mid-tidal) end of distribution of the adult snails and barnacle prey. Carriker (1957) observed that geotaxis of young snails is dependant on their state of hunger; unfed snails move upward while those that are satiated or exposed to food do not. Rheotaxis reported in this study and by Rittschof *et al.* (1983) is motivated by hunger and released by chemical cues associated with prey. Furthermore, rheotaxis stimulated by low concentrations of barnacle odor may be inhibited or out-competed by high concentrations of mussel or oyster odor. Thus, proximity or abundance of mussels or oysters, prey species first encountered by newly hatched and upwardly migrating snails, may inhibit or compete with the odor of more distant barnacles thereby arresting further upward migration. The combined effects of chemo-, geo-, and rheotaxes bring newly hatched snails within reach of prey in the lowest possible part of the mid-tidal region. Bertness (1977) and Butler (1979) have postulated similar integration of geotactic, photo-

orthokinetic, and predatory behaviors to account for the vertical distribution of two other murcids, *Nucella emarginata* and *N. lamellosa* (Gmelin). Clearly, behavioral integration of a complex mixture of abiotic cues and prey odors is an important aspect of the distribution and ecology of *Urosalpinx cinerea* and related predatory boring gastropods.

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